

UPPER PROTEROZOIC MICROFOSSILS FROM THE SUMMER ISLES, N.W. SCOTLAND

by ZHANG ZHONGYING

ABSTRACT. A structurally preserved and distinctive microbiota composed of sphaeromorphic acritarchs and filamentous microfossils has recently been recovered from shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles, N.W. Scotland. The dominant sphaeromorphs comprise single vesicles, plurivesicular aggregates, and envelopes containing up to several tens of vesicles. They closely resemble those occurring in shales of the Roper Group, Northern Territory, Australia. Detailed study of the variety of sphaeromorphs has revealed that they probably represent stages in the life cycle of a single species of coccoidal, endospore-forming pleurocapsalean blue-green alga *Torridoniphycus lepidus* gen. et sp. nov. The filaments are hollow tubes ranging from 1.5 up to 53.0 μm wide. They are assigned to the taxa *Eomycetopsis crassiusculum* (Horodyski) comb. nov., *Siphonophycus beltensis* Horodyski, *Siphonophycus* sp., and unnamed larger filaments. Most of them are interpreted as representing discarded sheaths of filamentous oscillatoriacean cyanobacteria, and are similar to those preserved in shales of the lower Belt Supergroup in the Little Belt Mountains, Montana, and the Dismal Lakes Group in Arctic Canada. This microbiota is thought to be of cyanophyte affinity. The low taxonomic diversity and high dominance of a few species may indicate an unusual and restricted aquatic ecosystem.

DURING the last twenty years, most studies of Precambrian life in North America and Australia have centred on microfossils preserved in stromatolitic cherts, which largely represent shallow-water, benthic mat communities (Diver and Peat 1979; Horodyski 1980). Microfossils have also been described from Precambrian shales. Such studies were mainly conducted in the Soviet Union (Timofeev 1966, 1973) and in western Europe (Vidal 1976, 1981). In recent years, however, the study of shale-facies microfossils in Precambrian rocks has increased immensely (Allison and Moorman 1973; Bloeser and Schopf 1977; Cloud, Moorman and Pierce 1975; Diver 1980; Ford and Breed 1973; Hofmann 1977; Hofmann and Aitken 1979; Hofmann, Hill and King 1979; Horodyski 1980; Horodyski, Donaldson and Kerans 1980; Javor and Mountjoy 1976; Knoll and Keller 1979; Knoll, Blick and Awramik 1981; Moorman 1974; Peat *et al.* 1978; Xing Yusheng and Liu Guizhi 1973). These shale-facies microfossils provide the opportunity to study Proterozoic life quite different in appearance from that preserved in stromatolitic chert.

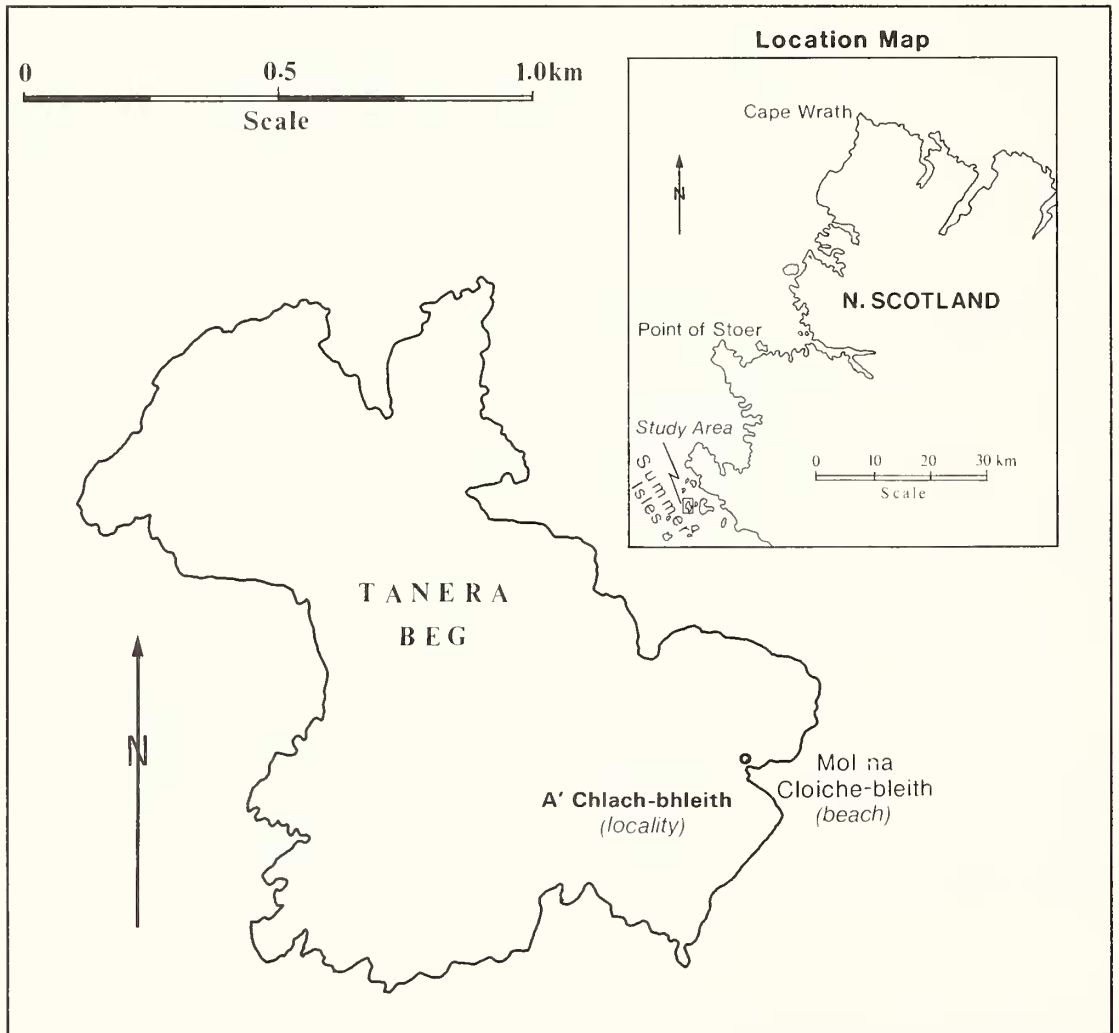
In 1979 P. R. Grant, W. L. Diver, and I made a reconnaissance of the late Proterozoic Aultbea Formation on Tanera Beg, Summer Isles, Highland Region, N.W. Scotland (text-fig. 1). A number of rock samples were collected from grey shales of the Aultbea Formation at different horizons (text-fig. 2). Structurally preserved microfossils, comprising sphaeromorphs and filaments, were found in petrographic thin sections and successfully recovered from macerations (Zhang Zhongying, Diver and Grant 1981). This occurrence prompted further collection of grey shales from some of the other Summer Isles for micropalaeontological investigation. During a return visit in 1980, Grant and Diver collected many samples from other shale horizons at the site of the initial discovery, and their collection was submitted to me for examination. The purpose of the paper is to illustrate, identify, and describe the microfossils from these samples.

GEOLOGICAL SETTING

The Torridon Group of N.W. Scotland consists of some 7 km of unmetamorphosed red beds, with subordinate grey shales (Stewart 1975). The group is separated from overlying Cambrian strata by an angular unconformity, and is itself divisible into four formations from the base upwards: (1) the Diabaig Formation; (2) the Applecross

Formation; (3) the Aultbea Formation; (4) the Cailleach Head Formation. Nearly all the grey shales of the group yield abundant microfossils. The underlying Stoer Group, over 2 km thick, also yields microfossils (Downie 1962; Cloud and Germs 1971). According to Downie, the Torridon Group is of upper Riphean age, and the Stoer Group of middle Riphean age (see Stewart 1975). There is a major unconformity between these two groups. Isotopic dating indicates a Rb-Sr whole-rock age of *c.* 777 Ma for the Torridon Group, and *c.* 968 Ma for the Stoer Group (Moorbath 1969; Stewart and Parker 1979) using the decay constant of Steiger and Jäger (1977). Therefore, the unconformity may indicate a long lapse in sedimentation.

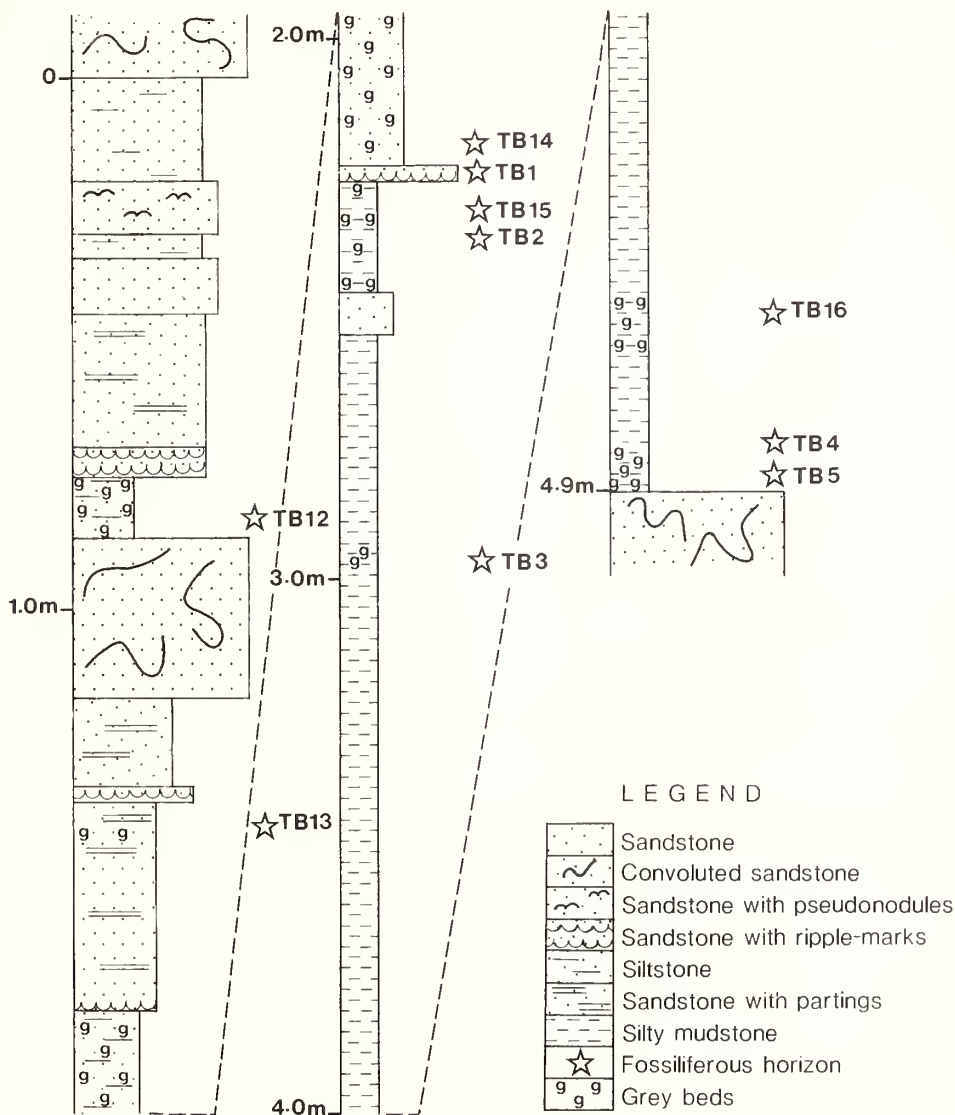
The Torridon Group outcrops extensively on the Summer Isles. Many of these islands and especially the greater part of Tanera Beg are composed of the Aultbea Formation, while the north-west end of Tanera Beg is formed by the Applecross Formation (Gunn 1907). The rock samples came from a grey shale unit in the Aultbea Formation, on the north-east side of A'Chlach-bhleith on the south-east corner of Tanera Beg, Summer Isles (NB 97080722, text-fig. 1). The shale unit, 4.9 m thick, mainly consists of purplish-grey silty mudstone, siltstone and sandstone, intercalated grey shales, and pink arkosic sandstone bands. Although the shale is generally silty, finer-grained intercalations of < 1mm-2cm also occur. Sixteen rock samples from ten horizons within the shale unit were collected (text-fig. 2). All contained organic walled microfossils, but the best preserved are found in the fine grey shales.



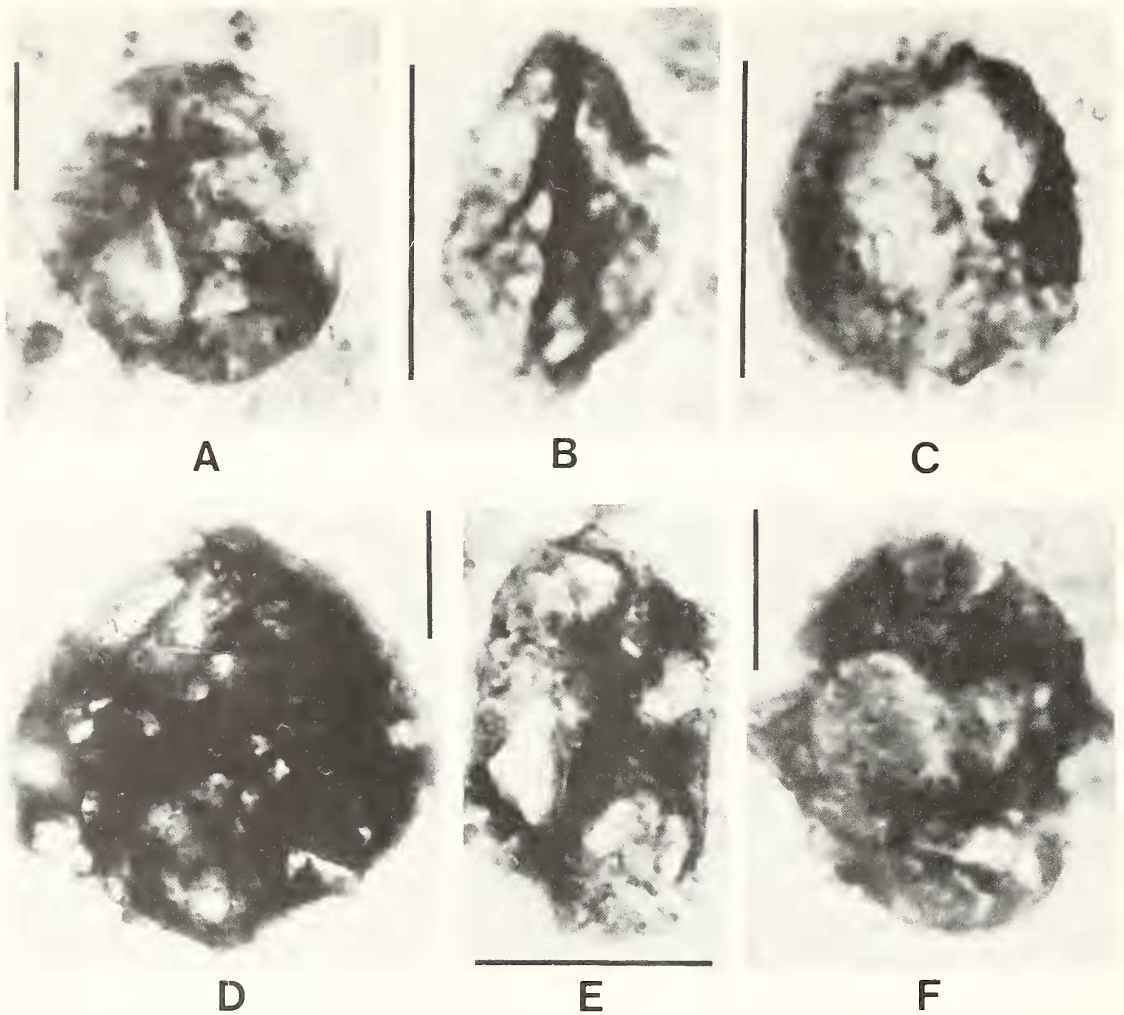
TEXT-FIG. 1. Index map with section location shown with black circle.

PREVIOUS MICROPALAEONTOLOGICAL INVESTIGATIONS

Several reports and descriptions of organic walled microfossils from grey shales of the Torridon Group in N.W. Scotland have been published (Teall 1907; Naumova and Pavlovsky 1961; Downie 1962; Diver 1980). The most detailed study of the Torridonian microbial assemblage has been carried out by W. L. Diver, and has advanced to the point at which relationships between sedimentological controls, palaeoecological factors, and microfossil distribution are being elucidated (Diver 1980; see also Zhang Zhongying *et al.* 1981). However, our knowledge about the fossil record from the Torridon Group of the Summer Isles remains very meagre, even though Gunn (1907) suggested that shale horizons there might contain microfossils.



TEXT-FIG. 2. Fossiliferous grey shale section at Mol na Cloiche-bleith, Tanera Beg. Section measured from the defined top.



TEXT-FIG. 3. Some compressed sphaeromorphic acritarchs (*Torridoniphyucus lepidus* gen. et sp. nov.) found in petrographic thin sections cut parallel to lamination. A, TB4-TS02, B8147; B, TB4-TS02, B8148; C, TB3-TS01, B8149; D, TB4-TS02, B8150; E, TB4-TS02, B8151; F, TB4-TS02, B8152. Scale bars in all photographs 10 μm .

METHODS

All rock samples collected were examined in petrographic thin sections and standard palynological macerations. Most petrographic thin sections were cut 30 μm thick, either perpendicular or parallel to lamination. Sometimes thicker thin sections were cut to avoid damaging the fossils. Most of the Tanera Beg fossils are compressed parallel to lamination, and so are readily studied in thin sections cut parallel to lamination (text-fig. 3). In thin sections cut perpendicular to lamination, the microfossils appear only as very thin dark streaks. Most microfossils are difficult to study in thin sections; the organic matter has undergone advanced stages of degradation, and the surrounding clastic sediment and diagenetic mineral crystals obscure and destroy their detailed structure. The microfossils preserved in thin sections of shale samples TB2, TB4, TB12, and TB16 are relatively better preserved and more abundant than the others.

Examination of petrographic thin sections shows that all these microfossils are within the bulk of the shale and are compressed parallel to lamination. These observations indicate that the microfossils are indigenous to the shale and syngenetic with deposition of the surrounding sedimentary matrix. The microfossils lie scattered on the bedding planes of the shale, and their preservation in thin sections is varied. It is likely that most of the microfossils had been carried away or washed around before being deposited with other detritus. The fact that all known filaments lack trichomes and many sphaeromorphs have no internal contents also supports this interpretation. It should be noted, however, that some of them might have been preserved close to their life position, even buried in the sediment during their growth and decay.

Detailed observations on their morphological structure were best carried out in hydrofluoric-acid-resistant residues. Rock samples were cut and the surface ground off on a rotary diamond lap to remove surface contamination and the silty parts of the rock as far as possible. From each sample 30–40 g of rock fragments bordered by fresh surface without obvious fractures were washed with distilled water, and left in 10% HCl until the supernatant was colourless. The HCl treatment usually took a few weeks, sometimes 2–3 months. Then, the fragments were broken down using a mixture of 10% HCl and 40% HF, the proportion of HF being gradually increased until only an organic sludge was left. This took 2–6 months depending on the mineralogy of the rock under investigation. The resulting macerate was washed with distilled water, mounted in glycerine jelly, and then examined in strew-slides under the light microscope. The best microfossils obtained from maceration came from the macerate of shale sample TB5.

Sixty-eight petrographic thin sections and 146 slides of macerates from different horizons in the shale unit on Tanera Beg were examined. Microfossils were measured using a micrometer on an optical microscope, and the dimensions obtained are accurate to within 0.5 μm . Counts were made along random, non-overlapping scan lines.

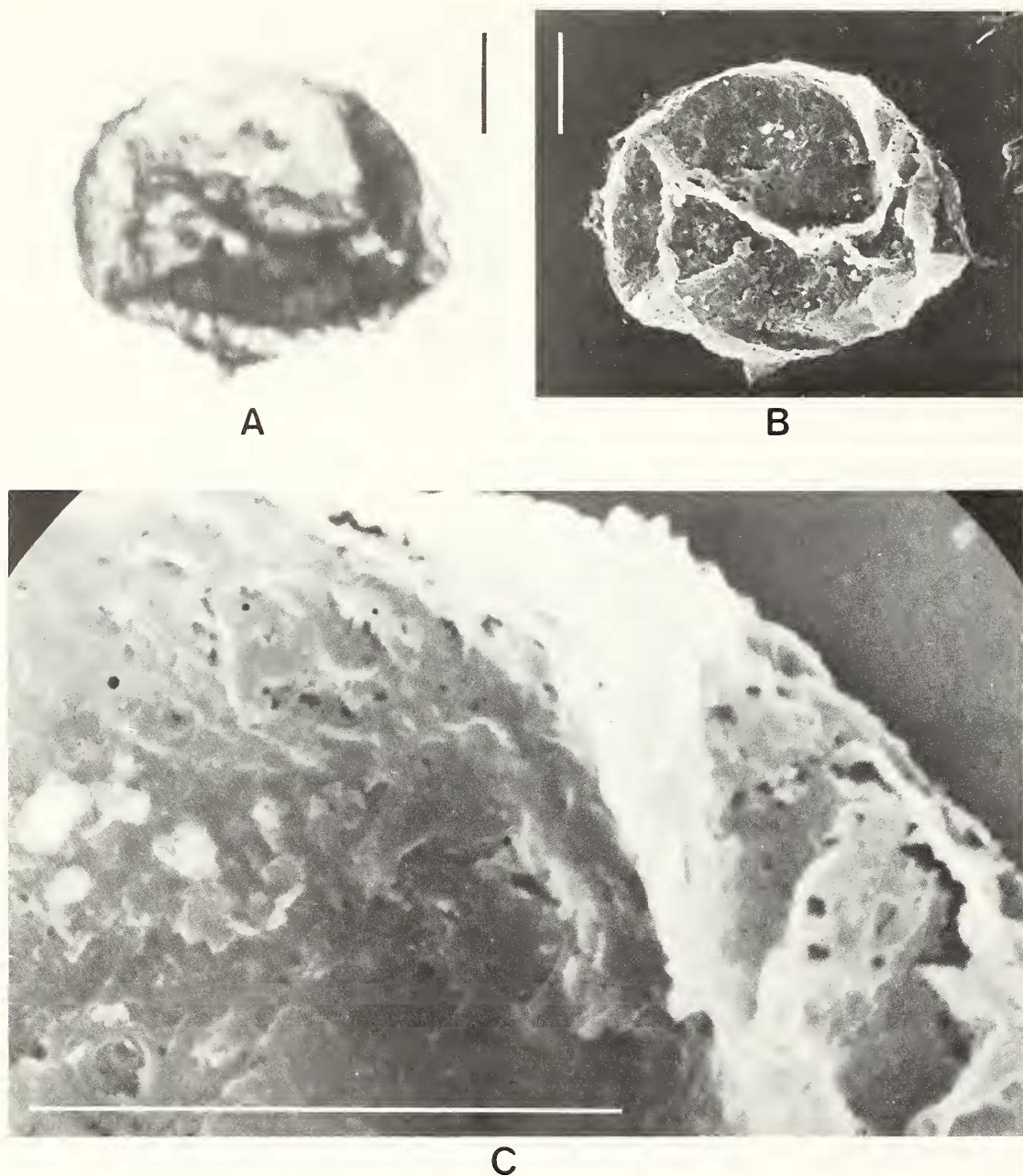
The taxonomic treatment of the Tanera Beg microfossils given below combines observations from petrographic thin sections and macerations. The sphaeromorphs illustrated in this study are mainly described from the macerate of shale sample TB5; it was chosen because it yielded a great variety of sphaeromorphs and the best preserved specimens. Shale sample TB5 also shows a representative and homogeneous fossil assemblage from a narrow stratigraphic interval at the base of the shale unit under study.

Many selected individual microfossils were picked out from the macerate of shale sample TB5 for comparative study by both light microscopy and scanning electron microscopy (text-fig. 4).

PALAEONTOLOGY

As discussed by many palaeontologists (Cloud and Germs 1971; Diver and Peat 1979; Hofmann *et al.* 1979; Loeblich and Tappan 1976; Peat *et al.* 1978; J. M. Schopf 1969; Vidal 1974, 1976), several factors render difficult the systematic study of Precambrian microfossils: (1) Different workers use different taxonomic schemes so that morphologically indistinguishable microfossils are assigned to different taxa. (2) Most specimens have undergone various stages of degradation and diagenesis, and diagnostic surface features have been subjected to modification and obliteration. (3) Invalid names continue to be used in the literature. (4) A great many studies have been conducted in the Soviet Union, but it is difficult to obtain publications and type specimens for study. (5) Comparisons are rendered very difficult by the low quality of the illustrations and the inadequate descriptions of many reports.

The Tanera Beg assemblage consists of two basic types of microfossils, namely the dominant sphaeromorphic acritarchs and the filamentous microfossils. Fossil sphaeromorphs are abundant in the Aultbea grey shales, and a variety of morphologies are evident. Early in the study of these sphaeromorphs, attempts were made to relate them to described material. On this basis they could be assigned to more than a dozen current taxa because of minor differences in preserved morphology, while some of them might be new forms. But this approach seems arbitrary, burdensome, and even unnecessary. An alternative is that most of the sphaeromorphs encountered (but not all) are variants of a single species, which is supported by evidence of continuous variation between morphotypes of the sphaeromorph microfossils, making it difficult to draw a definite line between them. Furthermore, some morphological features are clearly degradationally or preservationally related. Thus, it is reasonable to suppose that many of the Tanera Beg sphaeromorphs represent stages in the life cycle of a single species. Some of them are morphological variants caused by structural

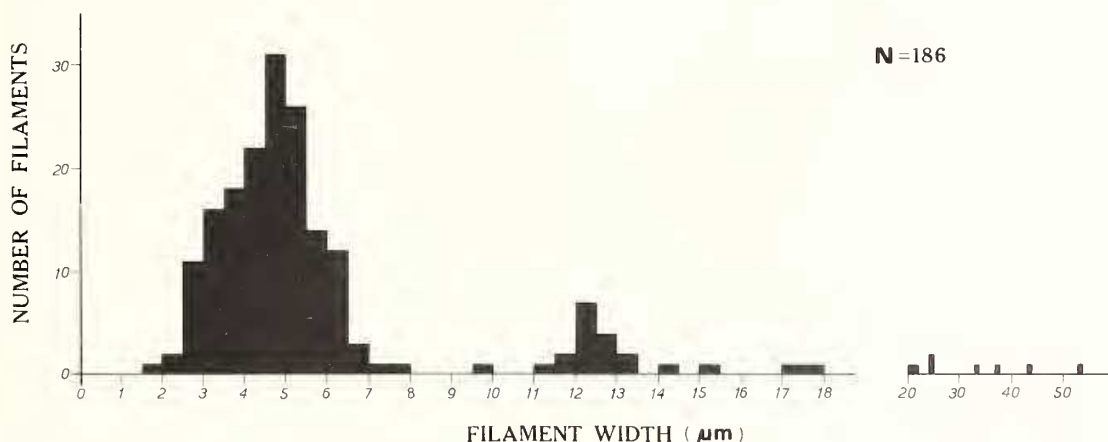


TEXT-FIG. 4. Comparative illustrations of the same single vesicle of *Torridoniphycus lepidus* gen. et sp. nov. in grey shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles (from the macerate of shale sample TB5), obtained by light microscopy (Zeiss photomicroscope III) (A, TB5-SEM10, B8153), and scanning electron microscopy (JEOL JSM-35) (B, and C showing detail of the surface of the same specimen). Scale bars in all photographs $10\mu\text{m}$.

degradation, compaction, and diagenetic alteration of an organism during fossilization. These post-mortem processes (Awramik, Golubic and Barghoorn 1972; Golubic and Hofmann 1976; Golubic and Barghoorn 1977; Golubic and Campbell 1979; Hofmann 1976; Knoll and Barghoorn 1975; Knoll, Barghoorn and Golubic 1975; Knoll and Golubic 1979) have undoubtedly played an important role in increasing morphological variation.

Comparisons with some modern and fossil endospore-forming blue-green algae help in interpreting the Tanera Beg sphaeromorphs. Beck (1963) described in detail the sequence of events in endospore formation of *Pleurocapsa fuliginosa* Hauck, which reproduces by simple binary fission, and by the production of endospores in two slightly different modes (see also Moorman 1974). From his description it is evident that a single species shows a wide size range and a variety of growth forms. Moorman (1974) took Beck's description of *P. fuliginosa* Hauck as a comparative model for interpreting the Hector microbiota from the Canadian Cordillera, and concluded that the microbiota was composed of a single species of endospore-forming blue-green alga described as *Sphaerocongregus variabilis* Moorman. Later Vidal (1976) emended the genus *Bavlinella* Shepeleva and transferred Moorman's species to *Bavlinella faveolata* (Shepeleva). It seems that this transfer is not warranted by present evidence and the two taxa are treated separately here. Knoll *et al.* (1981) followed Moorman (1974) in interpreting most of the microfossils in the Mineral Fork Formation, Utah, as stages in the life cycle of a single taxon, *B. faveolata* (Shepeleva) Vidal. Waterbury and Stanier (1978) described patterns of growth and development in pleurocapsalean cyanobacteria which support Moorman's interpretation; they placed in the Pleurocapsales all cyanobacteria which reproduce by the liberation of endospores formed through multiple fission. All of these important researches encouraged me to elaborate the diverse morphologies of the Tanera Beg sphaeromorphs and include most of them in a single species rather than to divide them arbitrarily into separate taxa.

The Tanera Beg filaments are most similar to those preserved in shales of the lower Belt Supergroup in the Little Belt Mountains, Montana (Horodyski 1980), and the Dismal Lakes Group in Arctic Canada (Horodyski *et al.* 1980). All preserved filamentous forms are apparently unbranched, originally tubular structures that were compressed during compaction of the surrounding clastic sediment. They range from 1.5 to over 50.0 μm wide, and lack cross walls or other evidence of cellular organization. In petrographic thin sections, they are brown to black in colour, and occur as both isolated filaments and fragments of filament aggregations. In some thin sections (shale sample TB4) cut parallel to lamination, their abundance reaches 41 filaments/cm². Measurements of 186 filaments in 15 sections reveal a bimodal size distribution (text-fig. 5). Filaments 1.5–8.0 μm wide comprise the



TEXT-FIG. 5. Size distribution of filamentous microfossils in grey shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles (186 filaments measured in 15 petrographic thin sections cut parallel to lamination).

primary mode of the distribution. Assuming an initially cylindrical shape, undeformed specimens in the Aultbea assemblage would be $1\text{--}5\ \mu\text{m}$ in diameter (= compressed width $\times 2/\pi$). Filaments less than $2\cdot5\ \mu\text{m}$ wide might be assigned to *Archaeotrichion* Schopf (1968). They are not formally described in this paper because of their rare occurrence. Filaments $2\cdot5\text{--}8\cdot0\ \mu\text{m}$ wide are here referred to *Eomycetopsis* Schopf (1968). The secondary mode is a rather small one, and its size range ($11\cdot0\text{--}13\cdot5\ \mu\text{m}$ in width) lies reasonably within a single taxon (*Siphonophycus beltensis* Horodyski). Larger filaments up to $53\ \mu\text{m}$ wide are also present, but they are not common. Most of the Tanera Beg filaments are here interpreted as representing discarded sheaths of oscillatoriacean cyanophytes.

All specimens illustrated in this paper are deposited in the Geology Department Type-Fossil Collection, Nanjing University, Nanjing, China, under catalogue Palaeobot. Coll., Nanjing Univ. B8111-8153. Rock samples and the macerate of shale sample TB5 are also housed at the British Museum (Natural History), London.

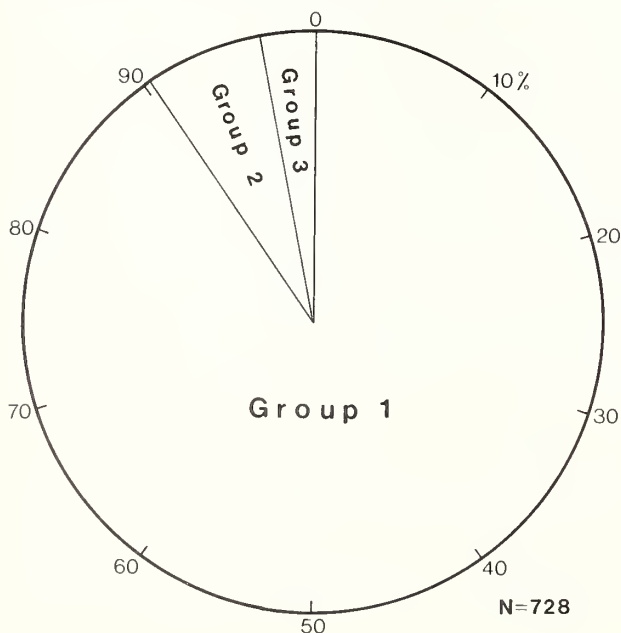
Division CYANOBACTERIA
Class COCOGONEAE
Order PLEUROCAPSALES
Genus TORRIDONIPHYCUS gen. nov.

Type species. *Torridoniphycus lepidus* sp. nov.

Derivation of name. From the Torridon Group.

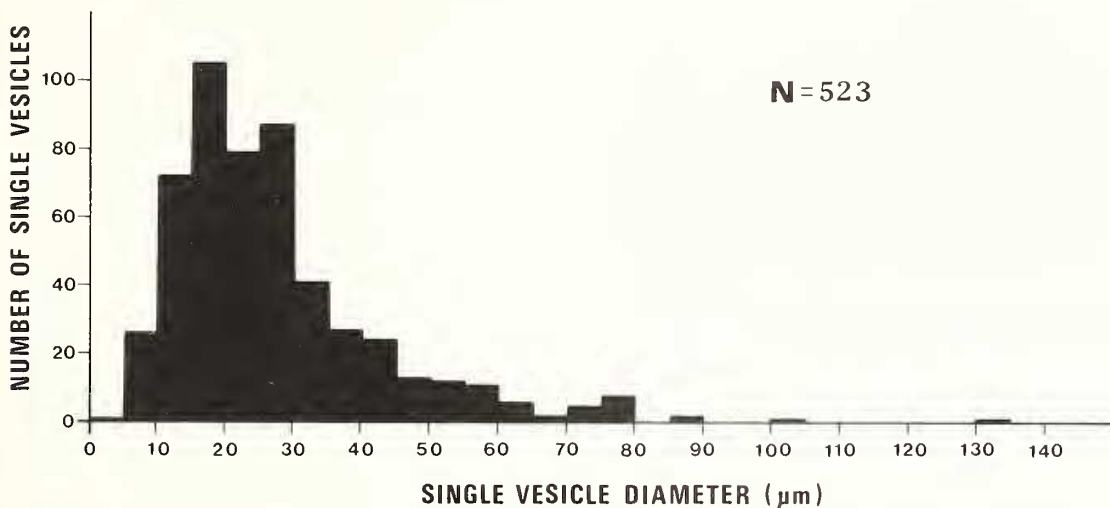
Diagnosis. The genus is composed of three distinctive morphological groups: (1) single vesicles; (2) plurivesicular aggregates; (3) envelopes containing many to several tens of vesicles. The first morphological group is the most abundant (text-fig. 6).

(1) Single vesicles, circular to elliptical, single-walled, light brown to black (Pl. 46, figs. 1-14; text-figs. 3, 4). They range in size from 4 to $125\ \mu\text{m}$ in diameter, but most fall within the range $10\text{--}25\ \mu\text{m}$ (text-fig. 7). Preserved surface texture chagrenate, psilate, granulate, scabrous, spongy, or microrugulose, often with various wrinkles and folds, or irregularly shaped mineral grain impressions or perforations. Many of the larger vesicles open by median splits. The original surface is



TEXT-FIG. 6. Relative proportions of three morphological groups (Group 1—90.4%, Group 2—6.5%, Group 3—3.1%) of *Torridoniphycus lepidus* gen. et sp. nov. in grey shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles (728 specimens counted in 42 slides from the macerate of shale sample TB5).

thought to be smooth to finely granulate; other surface textures and ornamented wrinkles and folds are probably preservational features resulting from degradation and post-sedimentary compaction. Small vesicles represented by those in text-fig. 3B, C, E, and Pl. 46, figs. 1, 6, 4–22 μm in diameter, are interpreted as spores or 'baeocytes' (Waterbury and Stanier 1978) released by endosporangia, or as 'nannocytes' (Fritsch 1945; Geitler 1960). Some of them might also represent stages in cell growth. The specimen in Pl. 46, fig. 11 shows a cell undergoing the degradation process. Its outer layer is interpreted as a sheath originally enclosing the cell, while the inner dark body represents coalesced and degraded remnants of the entire cell. Such specimens as those shown in Pl. 46, figs. 9, 12, 13 are taken as empty sheaths indicating the final products of the degradation process of independent cells, or endosporangial walls (Pl. 46, figs. 8, 10). It should be noted that larger vesicles in excess of 100 μm in diameter have been encountered, but these are exceedingly rare.



TEXT-FIG. 7. Size distribution of single vesicles of *Torridoniphycus lepidus* gen. et sp. nov. in grey shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles (523 single vesicles measured in 61 slides from the macerate of shale sample TB5).

(2) Plurivesicular aggregates, from 20 up to more than 100 μm across, consist of 4, 8, 16, and up to several hundreds of rounded vesicles. These aggregates (Pl. 46, figs. 15–18, 20, 22) are interpreted as representing the successive products of binary fission. Their outer gelatinous envelopes, if present, might be broken up during cell division. Cell division seems to be binary only. The individual vesicles, single-walled, 10.0–17.5 μm in diameter, are closely packed to form globose masses. Vesicles are diagenetically modified; the original surface is thought to be smooth to finely granulate. Inner dark bodies can also occur in some vesicles.

(3) Envelopes containing vesicles. This morphological group (Pl. 46, figs. 19, 21, 23, 24) is taken as representing events of ordinary endospore formation through multiple fission. The specimen in Pl. 46, fig. 21 is interpreted as an endosporangium, and those in Pl. 46, figs. 19, 23, 24 as incomplete endosporangia or their broken pieces with attached endospores. Endosporangia, 35–> 100 μm across, clearly contain up to several tens of spores. Endospores, spheroidal, 4–22 μm in diameter, are loosely or closely distributed within a common non-lamellar organic envelope. The envelope opens by median splits, and occasionally splits up into several sheets or ribbons with endospores still attached. The specimen in Pl. 46, fig. 8 shows a nearly empty endosporangial wall (group 1) and three spores being released from one end.

Discussion. Although this taxon closely resembles *Sphaerocongregus* Moorman in the morphologically variable growth forms, there are some important differences which justify a new genus: (1) *Sphaerocongregus* forms linear aggregates which are unknown in *Torridoniphycus*. (2) *Torridoniphycus* forms tetrads which have not been reported in *Sphaerocongregus*. (3) The outer envelopes of *Torridoniphycus* open by median splits which have not been seen in *Sphaerocongregus*. (4) Comparable individuals of *Sphaerocongregus* are much smaller in size than those of *Torridoniphycus*. However, the intermediate growth forms of the latter are more complete and abundant than the former.

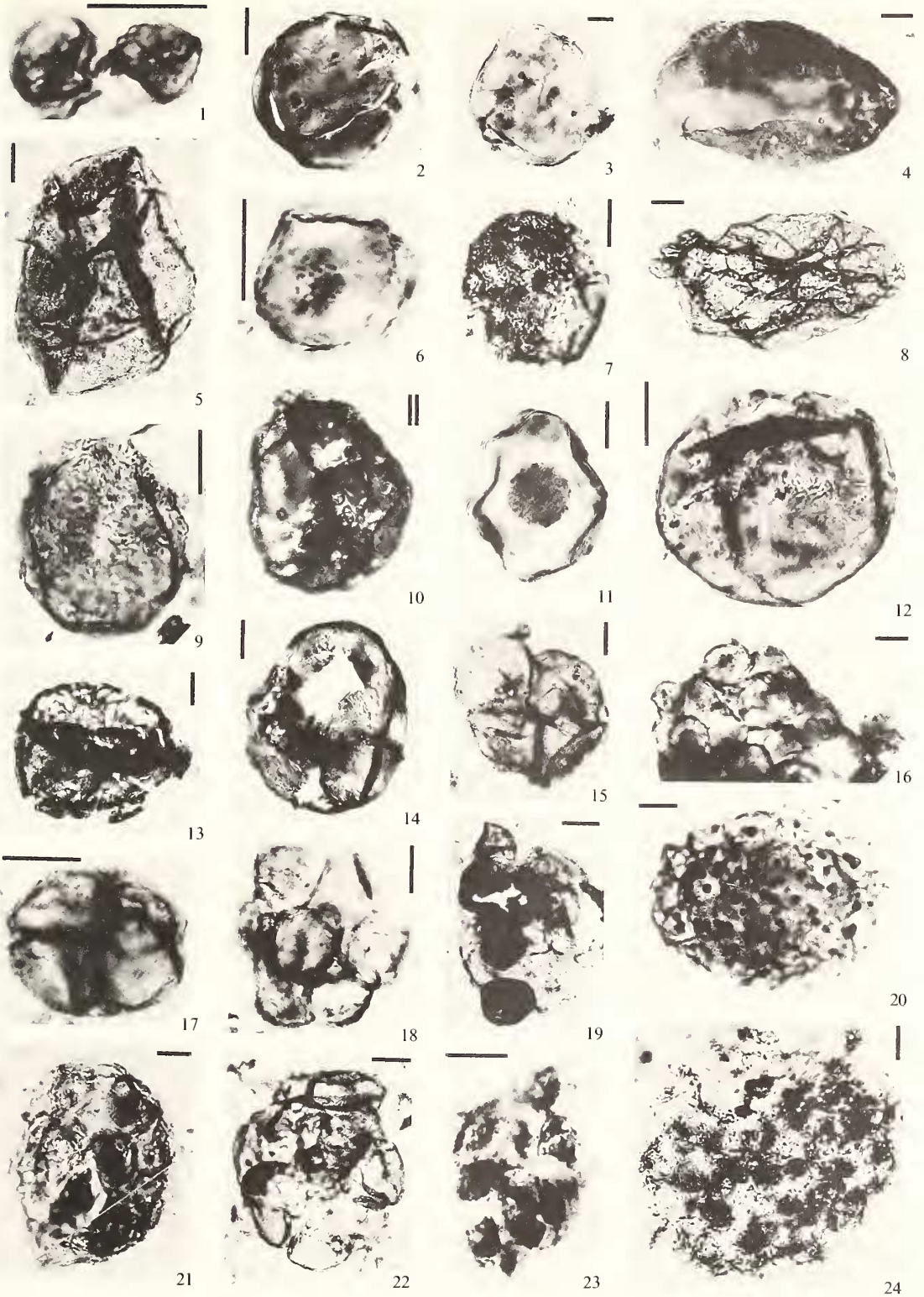
In her paper, Moorman (1974) referred *S. variabilis* to endospore-forming blue-green algae, but its exact taxonomic position was left in doubt. Later Cloud *et al.* (1975) concluded that *S. variabilis* was related to living entophysalidaceans, and had affinities with both the chroococcalean and chamaesiphonale cyanophytes. According to Knoll *et al.* (1981), the closer analogues to the Hector microbiota seem to be the genera *Xenococcus* and *Dermocarpa*, the latter having also been placed in the order Pleurocapsales by Waterbury and Stanier (1978).

I prefer to assign *Torridoniphycus* to the endosporangiate blue-green algae and more particularly to the order Pleurocapsales, but the possibility of affinities with higher algae, and especially Chlorophyta, still remains. In fact, endospore formation in the blue-green algae is very similar morphologically to aplanospore formation among the green algae (Cloud *et al.* 1975). Similarly, the Tanera Beg sphaeromorphs can also be classified in other ways. But a final solution is impossible without more comparable living analogues.

EXPLANATION OF PLATE 46

Structurally preserved sphaeromorphic acritarchs in grey shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles, Highland Region, N.W. Scotland. All specimens are acid-resistant residues obtained by hydrofluoric acid maceration from shale sample TB5. Photographs in figs. 3, 4, 8, 10, 16, 21, 24 were obtained using transmitted-light, dry-objective optics; all others using transmitted-light, oil-immersion optics. Figure 21 is a composite photograph. Single bar scale is 10 μm long; double bar scale 20 μm long. Slide number and the Paleobot. Coll. Nanjing Univ. number are given for each specimen. All specimens appear to represent possibly different developmental stages of a single taxon, *Torridoniphycus lepidus* gen. et sp. nov., interpreted as an endospore-forming pleurocapsalean blue-green alga.

Figs. 1–24. *Torridoniphycus lepidus* gen. et sp. nov., composed of single vesicles (figs. 1–14), plurivesicular aggregates (figs. 15–18, 20, 22), and envelopes containing many to several tens of vesicles (figs. 19, 21, 23, 24). 1, small vesicles (spores), TB5-MAC26, B8111. 2, chagrenate surface with narrow peripheral wrinkles, TB5-MAC44, B8112. 3, psilate to slightly granular surface, TB5-MAC15, B8113. 4, elliptical vesicle with scabrous or microrugose surface texture opens by a wide median split, TB5-MAC38, B8114. 5, vesicle with wrinkles and folds, TB5-MAC61, B8115. 6, vesicle with a more or less diffuse, granular inner body, TB5-MAC60, B8116. 7, scabrous to spongy surface texture, TB5-MAC32, B8117. 8, vesicle interpreted as a nearly empty endosporangial wall with three spores being released from one end, TB5-MAC25, B8118. 9, vesicle surface covered with very fine microfolds, TB5-MAC04, B8119. 10, large vesicle (endosporangial wall) having small and large perforations, TB5-MAC46, B8120. 11, vesicle containing a large granular inner body, TB5-MAC05, B8121. 12, vesicle surface with a few narrow folds and very fine microfolds, TB5-MAC53, B8122. 13, vesicle surface with irregularly shaped mineral grain impressions or perforations, TB5-MAC29, B8123. 14, vesicle surface with irregularly shaped openings, TB5-MAC28, B8124. 15, tetrad, TB5-MAC05, B8125. 16, plurivesicular aggregate consisting of tens of vesicles tightly compressed together, TB5-MAC01, B8126. 17, tetrad, TB5-MAC13, B8127. 18, plurivesicular aggregate (possibly 8), TB5-MAC46, B8128. 19, ribbon of vesicles, interpreted as a broken piece of endosporangium on which endospores are still attached, TB5-MAC32, B8129. 20, plurivesicular aggregate consisting of about a hundred vesicles, TB5-MAC05, B8130. 21, a well-defined envelope containing vesicles, interpreted as an endosporangium containing endospores, holotype, TB5-MAC29, B8131. 22, plurivesicular aggregate (possibly 16), TB5-MAC59, B8132. 23, vesicles (attached endospores) within a broken envelope (endosporangium), TB5-MAC26, B8133. 24, large sheet of vesicles, interpreted as a large piece of endosporangium on which endospores are still attached, TB5-MAC32, B8134.



It should be noted that among the diverse Tanera Beg sphaeromorphs it is difficult to distinguish between larger spores and smaller cells, between single enlarged cells in the final stage of degradation and endosporangial walls, and between ordinary endosporangia and those of the binary fission type if the latter are covered with an outer gelatinous envelope. However, it seems that ordinary endospore formation might be a fairly simultaneous process, different from the successive process of binary fission or 'nannocyte-formation' as described by Geitler (1925, 1960).

The genus *Torridoniphycus* is based on a series of well-preserved specimens representing various stages of the life cycle and occurring in the same horizon. A speculative reconstruction of the life cycle for the Tanera Beg sphaeromorphs (*Torridoniphycus lepidus* gen. et sp. nov.) is illustrated in text-fig. 8.

Torridoniphycus lepidus sp. nov.

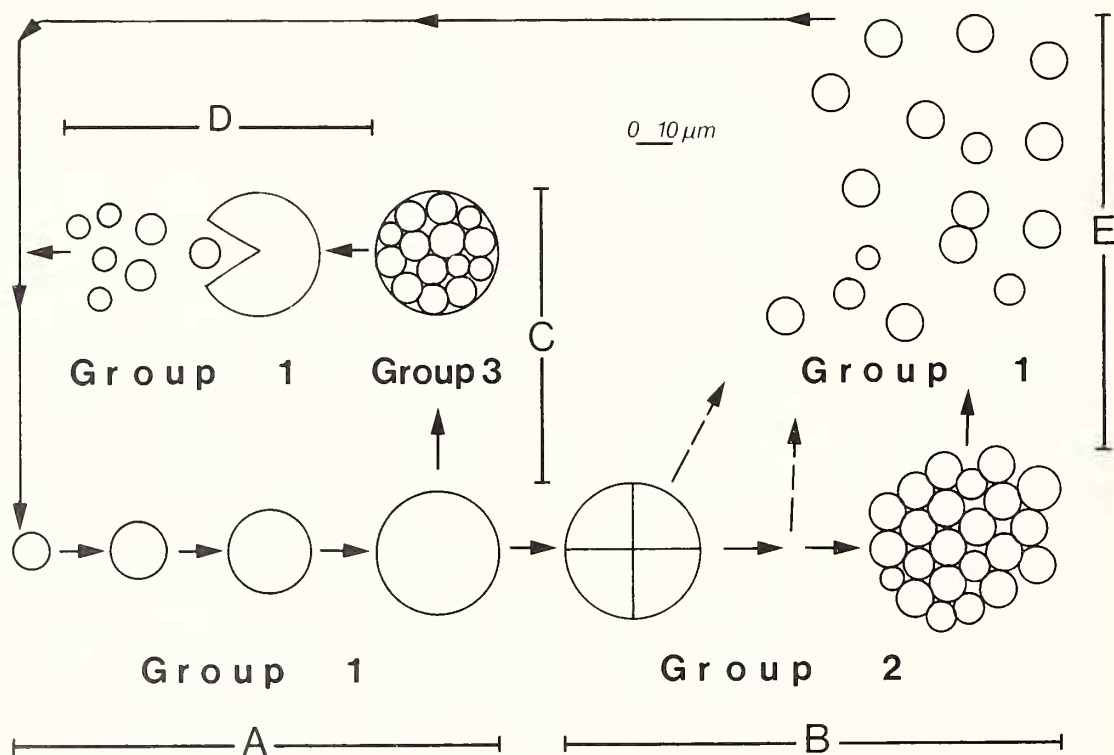
Plate 46, figs. 1-24; text-figs. 3, 4, 6, 7, 8

Type specimens. The fossil in Pl. 46, fig. 21 is cited as holotype (TB5-MAC29, B8131). All other specimens illustrated are paratypes.

Origin of name. After the delicate appearance of the type specimens.

Type locality and horizon. Shale sample TB5, near the base of a grey shale unit in the Aultbea formation, Torridon Group, on the north-east side of A'Chlach-bhleith on the south-east corner of Tanera Beg, Summer Isles, Highland Region, N.W. Scotland (NB 97080722).

Diagnosis. As for genus.



TEXT-FIG. 8. Hypothetical life cycle for *Torridoniphycus lepidus* gen. et sp. nov.: A, cell growth; B, repeated binary fissions; C, endospore formation through multiple fission; D, endospore (baecocyte) release; E, 'nannocyte' release.

Class HORMOGONEAE
Order OSCILLATORIALES

Genus *EOMYCETOPSIS* Schopf, 1968 emend. Knoll and Golubic, 1979

Type species. Eomycetopsis robusta Schopf, 1968, p. 684, pl. 82, figs. 2, 3; pl. 83, figs. 1-4.

Eomycetopsis crassiusculum (Horodyski, 1980) comb. nov.

Plate 47, figs. 3-6, 9-13; text-fig. 9

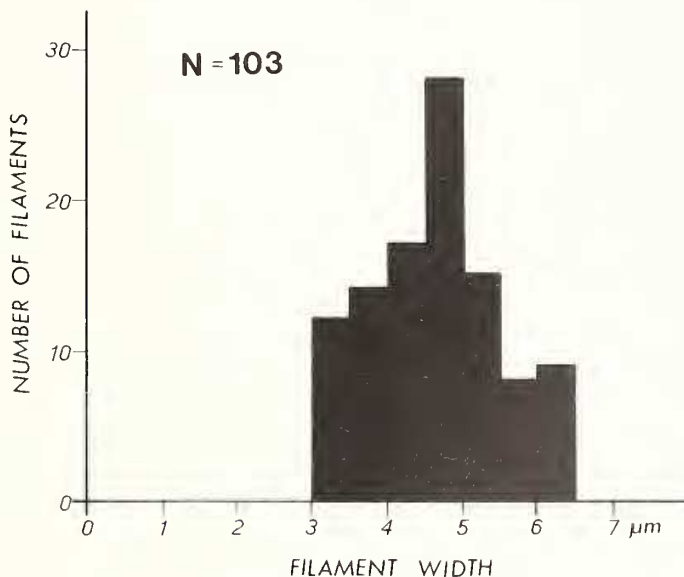
1980 *Siphonophycus crassiusculum* Horodyski, p. 656, pl. 1, figs. 6, 7.

1980 *Siphonophycus crassiusculum* in Horodyski, Donaldson and Kerans, p. 1166, fig. 3b-e.

Description. Filaments uniform, flattened, non-septate, unbranched, generally gently curved, occasionally flexed or twisted, up to 900 μm long, 3.0-6.5 μm across, width averaging 4.6 μm (103 filaments measured); solitary, or irregularly clustered. Walls less than 0.5 μm thick, dark brown to black; surface texture psilate to granulate.

Discussion. *Eomycetopsis* Schopf (1968) was originally thought to be marked by occasional septa. Re-examining the type specimens of this taxon, Hofmann (1976) found the supposed 'septae' to be folds or inflections in the wall of non-septate tube. Based on the discovery of cellular remnants and the recognition of the mat-like arrangement of tubule populations, Knoll and Golubic (1979) corroborated the suggestion of Hofmann, and formally emended the genus.

These filaments may represent flattened sheaths of oscillatoriacean cyanophytes closely resembling *Siphonophycus crassiusculum* Horodyski from the lower Belt Supergroup (Horodyski 1980) and the Dismal Lakes Group (Horodyski *et al.* 1980). Removing the effects of flattening ($2 \times \text{width}/\pi$), the diameters of the *S. crassiusculum* tubes would be 1.9-4.2 μm across, which falls within the size range given for *Eomycetopsis* Schopf (1968). Thus, Horodyski's species (3-7 μm wide) is here transferred to the genus *Eomycetopsis*. It is possible that *Eomycetopsis crassiusculum* (Horodyski) is a synonym of



TEXT-FIG. 9. Size distribution of *Eomycetopsis crassiusculum* (Horodyski) comb. nov. filaments in grey shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles (103 filaments measured in 11 petrographic thin sections cut parallel to lamination).

E. robusta Schopf and/or *E. filiformis* Schopf from the Bitter Springs stromatolitic cherts (Schopf 1968). Since there is no good basis to prove these to be conspecific, however, the continued use of these names will serve a useful purpose if each is restricted to the lithofacies from which it was originally described.

E. crassiusculum (Horodyski) is the most common filament in the shale of the Aultbea Formation of the Summer Isles.

Genus SIPHONOPHYCUS Schopf, 1968
Siphonophycus beltensis Horodyski, 1980

Plate 47, figs. 1, 2

Description. Filaments broad, compressed, non-septate, unbranched, generally gently curved, solitary, up to 250 μm long, 11.0–13.5 μm across, with wall less than 0.2 μm thick. Surface texture psilate, with irregular transverse markings.

Discussion. These filaments have the morphological characteristics of *Siphonophycus beltensis* Horodyski from the lower Belt Supergroup (Horodyski 1980) and the Dismal Lakes Group (Horodyski *et al.* 1980). These flattened tubes are best interpreted as preserved sheaths of oscillatoriacean algae, but all known specimens lack preserved trichomal contents.

Siphonophycus sp.

Plate 47, fig. 7

Description. Flattened fragments of simple, non-septate, unbranched filaments, 9.5–25.0 μm wide. Surface diagenetically modified, psilate to irregularly granulated; faint transverse markings in some places.

Discussion. These filaments probably represent the preserved empty sheaths of oscillatoriacean algae.

Unnamed Larger Filaments

Plate 47, fig. 8

Discussion. Filaments larger than 25 μm wide are rare in the Aultbea Formation of the Summer Isles. The largest fragment measured is 53 μm wide. These specimens resemble sheaths of extant *Lyngbya*-like oscillatoriacean cyanophytes.

EXPLANATION OF PLATE 47

Structurally preserved filamentous microfossils in grey shales of the Aultbea Formation, Torridon Group, on Tanera Beg, Summer Isles, Highland Region, N.W. Scotland. Specimens shown in figs. 2, 3, 6, 7, 8, 13 are acid-resistant residues obtained by hydrofluoric acid maceration; all others are in petrographic thin sections cut parallel to lamination. Photographs in figs. 3, 4, 5, 11, 12 were obtained using transmitted-light, oil-immersion optics; all others using transmitted-light, dry-objective optics. Figures 12 and 13 show composite photographs. Single bar scale is 10 μm long; double bar scale 20 μm long. Thin section (or slide) number and the Paleobot. Coll. Nanjing Univ. number are given for each specimen. All specimens appear to represent discarded sheaths of oscillatoriacean cyanophytes.

Figs. 1, 2. *Siphonophycus beltensis* Horodyski. 1, TB4-TS506, B8135. 2, TB5-MAC10, B8136.

Figs. 3–6, 9–13. *Eomycetopsis crassiusculum* (Horodyski) comb. nov. 3, TB5-MAC16, B8137. 4, TB4-TS502, B8138. 5, TB2-TS101, B8139. 6, TB5-MAC06, B8140. 9, TB2-TS101, B8141. 10, TB4-TS503, B8142. 11, part of the specimen in fig. 10. 12, TB4-TS504, B8143. 13, TB5-MAC06, B8144.

Fig. 7. *Siphonophycus* sp., TB5-MAC08, B8145.

Fig. 8. Unnamed larger filament, TB5-MAC16, B8146.



ZHANG ZHONGYING, Precambrian filamentous microfossils

DISCUSSION AND SUMMARY

The *c.* 800 Ma old Tanera Beg microbiota is composed of two basic types of microfossils, namely the dominant sphaeromorphs and the filaments. Although the sphaeromorphs show a variety of morphologies, this microbiota is of low taxonomic diversity. The sphaeromorphs are completely dominated by various growth forms of a single taxon, *Torridoniphycus lepidus* gen. et sp. nov., which is thought to be an endospore-forming pleurocapsalean blue-green alga, which might have grown as epiliths on rocks. Most of the filaments are interpreted as representing discarded sheaths of oscillatoriacean cyanobacteria, and might have been planktonic. Thus, the Tanera Beg microbiota is most likely of cyanophyte affinity.

The sandstone of the Torridon Group is generally thought to be of fluvial origin, but much debate has centred on the depositional environment of the grey shales in the group. Some geologists considered that the environment was tidal (Peach *et al.* 1907, p. 325), tidal marine (Allen *et al.* 1960), and marine (Stewart 1969), while others described it as fresh water, such as lacustrine (Selley 1965*a, b*). By using a refined version of the boron palaeosalinity indicator, Stewart and Parker (1979) concluded that the grey shales in the Stoer and Torridon groups are non-marine. As modern pleurocapsalean algae have a wide natural distribution, occurring in terrestrial, freshwater, and marine environments (Golubic 1976; Waterbury and Stanier 1978), the occurrence of the Tanera Beg sphaeromorphs and filaments cannot give any particular interpretation strong support. However, the salinity of the water is uncertain. The low taxonomic diversity and the high dominance a few species of the microbiota may indicate an unusual and restricted aquatic ecosystem, such as a marine embayment or a lake.

Some sphaeromorphs of the Tanera Beg assemblage are similar to those described from Middle and Upper Proterozoic shales in the Soviet Union (Timofeev 1966, 1973), Sweden (Vidal 1974, 1976, 1981), Australia (Peat *et al.* 1978), Canada (Hofmann and Aitken 1979; Horodyski *et al.* 1980), and the United States (Horodyski 1980). Among these microbiotas, the Tanera Beg sphaeromorphs closely resemble, on the whole, those occurring in the *c.* 1300–1400 Ma shales of the Roper Group, Northern Territory, Australia (Peat *et al.* 1978). It appears that many sphaeromorphic forms of the Roper microbiota might also be interpreted as representing stages in the life cycle of a *Torridoniphycus*-like alga. As far as the Tanera Beg filaments are concerned, they are remarkably similar to those preserved in shales of the *c.* 1400 Ma lower Belt Supergroup in the Little Belt Mountains, Montana, and the *c.* 1200 Ma Dismal Lakes Group in Arctic Canada. As mentioned above, the Torridon Group has been dated at *c.* 800 Ma. If these isotopic age data are correct, the similarities between these microbiotas probably reflect the widespread occurrence of oscillatoriacean cyanophytes and *Torridoniphycus*-like algae during Middle and Late Proterozoic time.

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